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EDITORIAL

Conservation biogeography – foundations, concepts and challenges

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ABSTRACT

Conservation biogeography involves the application of biogeographical principles, theories, and analyses to problems regarding biodiversity conservation. The field was formally defined in 2005, and considerable research has been conducted in the ensuing 5 years.

This editorial sets the context for 16 contributions in a special issue of *Diversity and Distributions* on developments and challenges in conservation biogeography. Papers are grouped into the following main themes: species distribution modelling; data requirements; approaches for assigning conservation priorities; approaches for integrating information from numerous disparate sources; special challenges involving invasive species; and the crucial issue of determining how elements of biodiversity are likely to respond to rapid climate change. One paper provides a synthesis of requirements for a robust conservation biogeography for freshwater ecosystems.

Conservation biogeography is well poised to make a significant contribution to the process of providing policy makers with objectively formulated scenarios and options for the effective management of biodiversity. The editorial, and the papers in the special issue, deliberate on many of the exciting developments in play in the field, and the many complex challenges that lie ahead.

Keywords

Biological invasions, climate change, conservation planning, data requirements, invasion ecology, species distribution modelling.

INTRODUCTION

Conservation biogeography was formally defined in the pages of this journal by Whittaker *et al.* (2005) as the application of biogeographical principles, theories and analyses (being those concerned with the distributional dynamics of taxa individually and collectively) to problems concerning the conservation of biodiversity. The field aims to support conservation practices by providing improved theoretical insights and practical methods for the many things that conservation managers need to do: design reserve networks, plan and implement ecological restoration, manage invasive species, reintroduce species where and when deemed necessary and appropriate. There is increasing realization that conservation at small scales is not sufficient for the task at hand.

The issue that carried the Whittaker *et al.* (2005) paper also launched this journal's current direction with the subtitle: *A Journal of Conservation Biogeography* (Richardson, 2005). In the ensuing 5 years, many journals have carried important contributions on the emerging discipline of conservation biogeography. As of 23 February 2010, the Whittaker *et al.* (2005) paper had been cited 123 times (ISI Web of Knowledge). Fifty-six percent of citations were in the main biogeography and conservation biology journals: *Journal of Biogeography* (18%), *Diversity and Distributions* (15%), *Biodiversity and Conservation* (10%), *Ecography* (6%), *Biological Conservation* (4%) and *Conservation Biology* (3%). The remaining citations appeared in another 42 journals. The top ten countries represented in address lists in the papers citing Whittaker *et al.* (2005) were (in order): USA, UK, Spain, Brazil, Italy, Australia, Portugal, France, Norway and South Africa. The need for insights from biogeographical studies to inform conservation actions is clearly widely recognized, and much research effort is focussing in this area in many parts of the world (Table 1). Biogeographical insights from all these areas are important for almost every facet of conservation management. To manage biodiversity, we need to know where it is, how it is arranged at different spatial scales, how the different facets of diversity co-vary in space and time and how they respond to a bewildering suite of drivers that act

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Table 1 Prominent areas of research in conservation biogeography.

The biogeography of degradation (habitat fragmentation, homogenization, urbanization and other human-induced impacts)
Processes (colonization, climate as a fundamental determinant of distribution, dispersal, disturbance, extinction, persistence, range expansion, resilience, speciation)
Inventory, mapping and data issues (atlas data, breeding bird surveys, citizen science, detectability/discovery probabilities, herbaria and other collections, sampling intensity and biases)
Species distribution modelling (bioclimatic modelling, habitat-suitability analysis, model performance, niche-based models, presence-only data vs. presence-absence data, dispersal kernel analysis)
Characterizing biotas (conservation status, diversity indices and patterns, ecoregions, endemism, rarity, range size, species–area relationships, threatened species, identification of alternative baselines from long-term ecological data)
Conservation planning (complementarity, congruence, conservation units, ecosystem services, gap analysis, global conservation assessments, irreplaceability, reserve networks, surrogates)
Methods (molecular methods, palaeoecology, remote sensing, scenario development)
Related fields (global change biology, invasion ecology, bioinformatics, molecular phylogenetics, network analysis, re-introduction ecology, risk analysis, behavioural ecology, population viability analysis)
Overarching themes: niche (fundamental vs. realized), novel climates/ecosystems, scale issues, uncertainty, Linnean shortfall, Wallacean shortfall)

and interact to mediate diversity and distributions via innumerable mechanisms and processes. Of increasing importance is the need for procedures and tools to facilitate the efficient utilization of large amounts of data from a wide range of sources. Also needed are efficient ways of evaluating uncertainty and the degree of bias in original data and outputs from predictive models or reserve-selection algorithms.

Whittaker *et al.* (2005) emphasized that knowledge about biodiversity remains inadequate because most species living on Earth are still not formally described ('the Linnean shortfall') and because geographical distributions of most species are poorly understood ('the Wallacean shortfall'). Research is progressing on numerous fronts, and much progress is being made in many areas. This issue of *Diversity and Distributions* presents a collection of 16 papers that address central issues in conservation biogeography. Half of the papers were specially solicited from members of the editorial team of the journal, who were asked to address what they identified as one of those central issues. The other half of the collection comprises another four solicited papers from prominent researchers and teams in the field (Ackerly *et al.*, 2010; Cadotte & Davies, 2010; Olden *et al.*, 2010 and Sexton *et al.*, 2010) and four papers that were submitted as normal contributions to the journal but which were deemed to address central issues appropriate for the theme: 'Conservation biogeography – foundations, concepts and challenges'.

The papers in the special issue may be grouped into the following broad themes (with some belonging in more than one category): species distribution modelling (Franklin, 2010; Gallien *et al.*, 2010; Scoble & Lowe, 2010); data requirements (Devictor *et al.*, 2010; Robertson *et al.*, 2010); approaches for assigning conservation priorities (Cadotte & Davies, 2010; Ferrier & Drielsma, 2010; Kraft *et al.*, 2010); approaches for integrating information from numerous disparate sources (Cumming *et al.*, 2010; Ferrier & Drielsma, 2010; Roura-Pascual *et al.*, 2010; Sexton *et al.*, 2010); special challenges involving invasive species (Gallien *et al.*, 2010; Leung *et al.*, 2010; Thuiller *et al.*, 2010); and the crucial issue of determining how elements of biodiversity are likely to respond to rapid climate change (Ackerly *et al.*, 2010; Franklin, 2010; Thomas, 2010). One paper provides a synthesis of requirements for a robust conservation biogeography for freshwater ecosystems (Olden *et al.*, 2010). The rest of this editorial sketches the context of these contributions within the field of conservation biogeography and suggests some profitable avenues for future work.

SPECIES DISTRIBUTION MODELLING – TOWARDS THE EFFICIENT INCORPORATION OF PROCESSES

Attempts to model the distribution of species (a key requirement for conservation biogeography) have proliferated in the past few decades, thanks to major advances in computer technology, analytical methods, the increasing availability of biological and environmental data and the increasing demand for prediction of species ranges under different scenarios (Guisan & Thuiller, 2005; Franklin, 2009). Maps of species distributions or habitat suitability are fundamental requirements for many aspects of conservation planning and management. Many different types of species distribution models (SDMs) have been developed to describe both the species niche and the suitability of a habitat to support a species. Various sub-types of bioclimatic-, niche-based, or 'envelope' models have been useful, but they have important limitations (Thuiller *et al.*, 2008). To meet the growing needs of conservation biogeography in an increasingly complex world, we need to move beyond static SDM predictions to incorporate key dynamic processes determining species distributions (Franklin, 2010; Gallien *et al.*, 2010). Franklin (2010) discusses three strategies of increasing complexity: models of species migration, models of community dynamics and models of population viability. There are exciting opportunities to refine the outputs of SDMs by incorporating parameters that mediate metapopulation demography and landscape interactions, life history traits, species interactions and the consideration of evolutionary history. Scoble & Lowe (2010) show that studies using molecular markers could profitably be incorporated into SDMs to help identify, for example, biogeographic barriers that may limit species movement. They discuss the scope for statistical phylogeography to be used for testing alternative hypotheses of species and community response to biogeographical processes associated with historical climatic extremes. Molecular marker approaches clearly offer exciting opportunities to advance our understanding of historical range change dynamics and for elucidating contemporary population demography and its relationship to changes in land use. Contemporary gene flow barriers and source-sink dynamics are undoubtedly important mediators of range dynamics. Although the dynamics of these factors will also change, adding insights from molecular approaches, such as landscape genetics, to SDMs could improve our ability to provide realistic models of species ranges under climate change and other components of global change.

Predicting range limits and changes in distribution of invasive non-native species is an important component of conservation planning and management in most ecosystems. A fundamental problem when modelling range dynamics of invasive species is that the organisms are, by definition, recent arrivals and are thus not in equilibrium with environmental conditions in the invaded region (Rouget *et al.*, 2004). New ways of looking at fundamental and realized niches in the native and invaded ranges are needed. Gallien *et al.* (2010) describe the emergence of a new generation of 'hybrid' models that incorporate the strengths of a range of different types of approaches, including curve-fitting models, matrix population models, metapopulation models, cellular automata, landscape models, individual-based models, mechanistic niche models and habitat-suitability models. Tailoring models to provide the best possible prediction of invasive species ranges is an area of intense research effort, and insights from this work will benefit species distribution modelling in general.

DATA REQUIREMENTS – ISSUES OF QUALITY AND QUANTITY

The shortage of high-quality data on the distribution of organisms is one of the biggest challenges facing conservation biogeographers. Data quality determines the type of model that can be used and the level of confidence that can be attached to model outputs. Factors that influence the quality of data, especially for species distribution modelling but also for other facets of conservation biogeography and related fields, include issues relating to spatial scale (grain/focus, extent, sample density, measurement scale), sampling design (sample size and resolution, prevalence, etc.) and temporal sampling (detectability, availability of historical data) (e.g., Franklin, 2009). Carefully designed sampling strategies and the use of remote sensing, automated sensors and other high-tech methods have radically improved the quality of biological data, and many online databases have created invaluable resources for conservation biogeography. There is, however, a never-ending quest to improve the quality and completeness of biological data. Two papers in this special issue address issues relating to ways of acquiring data for conservation biogeography. Devictor *et al.* (2010) describe a general framework highlighting the prerequisites of a dataset for conservation biogeography and examine the extent to which citizen science programmes (those involving data collection by the general public) fulfil these requirements. They show that many successful projects are underway in many countries and highlight five key factors associated with success: simplicity, a clear scheme linking key requirements for data and the capacity and interests of the project, feedback, communication and sustainability. Many impressive data-gathering ventures are underway in many parts of the world, but careful assessments of potential uses of the data can increase the value of such data (see also Foxcroft *et al.*, 2009). Atlas projects have an important role to play in collecting and managing high-quality distributional data that can be applied to a range of issues in conservation biogeography. Robertson *et al.* (2010) highlight the growing importance of atlas projects for conservation biogeography and suggest ways in which these datasets could be improved (see also Graham *et al.*, 2004).

ASSIGNING CONSERVATION PRIORITIES – INCLUDING ECOLOGICAL AND EVOLUTIONARY PROCESSES

Great strides have been made in recent decades towards developing methods for the objective assignment of priority for conservation to different regions and taxa. Systematic conservation planning is a growing field of study, with increasingly sophisticated methodologies (Margules & Sarkar, 2007). Older methods that relied exclusively on the analysis of static patterns of biodiversity components are now being replaced by protocols that incorporate ecological, evolutionary and landscape-level processes that generate the biodiversity and that are crucial for its maintenance and conservation. Whittaker *et al.* (2005) emphasized that conservation plans must strike a balance between focussing on patterns of current-day diversity (the compositionalist approach) with an understanding of the dynamic processes shaping the generation and loss of biodiversity (the functionalist approach) (and see Ladle & Whittaker, in press). A paper in this issue presents a state-of-the-art analysis of the effectiveness of the current protected area network in one of the world's most biologically rich and threatened terrestrial ecoregions – the California Floristic Province. Kraft *et al.* (2010) used data on range size and molecular-based estimates of taxon age to identify areas with high proportions of young and restricted-range taxa (areas that may represent evolutionary hotspots where historical or biogeographic features promote evolutionary diversification). They found that diversity measures were poorly correlated with climate and topographic heterogeneity (traditionally assumed to be associated with high biodiversity; Kreft & Jetz, 2007), and that substantial portions of the region with high levels of plant neoendemism fall outside protected areas. In another paper, Cadotte & Davies (2010) conducted a global review of methods used to encapsulate phylogenetic diversity and distinctiveness, and provide insights into how geographical commonness and rarity can be combined with these measures for conservation planning. The advent of rapid molecular DNA-sequencing technologies has led to a phylogenetic revolution, with large advances in both the amount and quality of information on species phylogenies, depicting their evolutionary relationships, and phylogenetic analysis methods. The evolutionary value of species or habitats can now be easily quantified for large clades, paving the way for the widespread use of evolutionary distinctiveness in conservation planning algorithms (e.g. Forest *et al.*, 2007).

Ferrier & Drielsma (2010) present a logical and flexible foundation for integrating disparate pattern- and process-related factors into conservation assessments in dynamic, multiple-use landscapes. Their approach comprises three broad modelling components. The first addresses the future condition of habitat across a landscape as a function of the present state, current and projected pressures acting on this, and any proposed, or implemented, management interventions. The second uses spatially explicit prediction of future habitat state to model the level of persistence expected for each of a set of surrogate biodiversity entities. The third component then merges these individual expectations to predict the overall level of persistence expected for overall biodiversity. This approach offers a unified overarching protocol for integrating different combinations of modelling techniques to serve the specific needs of different planning applications.

INTEGRATING INFORMATION FROM NUMEROUS DISPARATE SOURCES

A huge amount of information in many forms is available to conservation managers. The challenge is to design frameworks and platforms for the effective use and integration of such data to inform conservation planning and management. Three papers in this issue describe innovative strategies for the effective use of different types of data. Cumming *et al.* (2010) argue that network analysis provides an appropriate framework for integrating knowledge between the increasing number of disciplines involved in determining and deciding on conservation options. Underpinning their essay is the notion that the basic form of the mathematical representation of networks is the same for social and ecological systems (despite marked differences in the nature of the nodes and the connections). Consequently, they suggest network analysis provides an appropriate common language for quantifying and analysing similarities and differences between relational patterns in social and ecological systems and for understanding linkages and feedbacks within socio-ecological systems.

Many types of decision-support models are applied to guide management strategies when problems are complex. The systematic evaluation of risks and decisions in conservation management is a relatively new field (Burgman, 2005). The robustness of decision-making processes is rarely explicitly evaluated, and the influence of decision criteria in management decisions is seldom considered. In conservation management, this means that applied models have little heuristic value. Consequently, most decision iterations effectively start from ground zero. Managing invasive species is one of the most taxing challenges facing conservation managers in many parts of the world (Pyšek & Richardson, 2010). Roura-Pascual *et al.* (2010) describe a protocol for spatially explicit sensitivity analysis of typical decisions facing managers of invasive species in a complex environmental and socio-political setting. They take as an example the profound challenges posed to management by invasive plants in South Africa's Cape Floristic Region (Roura-Pascual *et al.*, 2009). Their scheme is developed to provide objective guidelines, in the form of static priority maps. They show that one factor ('area burnt recently') provided unequivocally important information for the effective management of invasive plants in this region, but that other factors demanded context-specific evaluation since levels of sensitivity were highly dependent on different features of the landscape, especially the spatial heterogeneity of particular factors.

A massive challenge facing humanity is that, according to most experts, even the most stringent mitigation of the causes of climate change will not avert radical impacts on biodiversity in the next few decades (IPCC, 2007). Consequently, conservation biogeographers will increasingly be called upon to inform sensible strategies for adaptation – practical measures for anticipating or reacting to the impacts of climate change. As in other spheres of conservation science (e.g. Richardson *et al.*, 2009), but acutely so in this arena, protocols are urgently required to guide conservation planners in how to merge data and perspectives from a wide range of stakeholders in a transparent and objective fashion. Issues relating to socio-cultural vulnerability and adaptive capacity must be placed on the table and evaluated alongside traditional conservation metrics when considering options for conservation action. Sexton *et al.* (2010) emphasize the need for combining geographies of socio-cultural adaptation and biodiversity risk to create workable global change conservation strategies.

SPECIAL CHALLENGES INVOLVING INVASIVE SPECIES

Conservation assessments increasingly need to consider the current and future role of invasive species. Understanding and modelling distributions of non-native species poses a special set of challenges, as mentioned previously. A range of fundamental questions relating to the ability of introduced species to establish and form self-sustaining populations in new areas are the focus of much research effort (Richardson & Pyšek, 2008). Among these questions are two that can be traced back to the writings of Charles Darwin, the resolution of which is an important quest for invasion ecologists and conservation biogeographers alike. The degree of relatedness of invaders to components of native communities (originally formulated in terms of taxonomic relatedness but now extended to phylogenetic relatedness) is predicted to promote naturalization because of niche adaptation. On the other hand, relatedness has been predicted to reduce naturalization because of niche overlap with native species ('Darwin's naturalization hypothesis'). Thuiller *et al.* (2010) review the studies that have tested these ideas. They argue that most of the inconsistency in this literature is attributable to discrepancies in the conceptual frameworks and analytical approaches applied in these studies, rather than to fundamental differences between model organisms and ecological contexts. They suggest that resolution of these questions requires close attention to appropriate phylogenetic and spatial scales, metrics, null models and measures of (dis)similarity.

Biological invasions provide a plethora of fundamental questions to challenge the ingenuity of conservation biogeographers. Leung *et al.* (2010) address a particularly important and interesting one – the issue of delimiting the range of an introduced organism. This is arguably the first step needed to enable managers to devise and implement barriers, apply strategies to slow spread or take other actions to prevent large-scale invasions. They distinguish three stages to identify the potential bounds of an invasion which they term Approach, Decline, Delimit (ADD). Their ADD algorithm uses general characteristics of the invasion pattern obtained during a search for occupied sites, combined with insights from sampling and probability theory, to delimit the invasion. They compare the outcome of the ADD analysis with four 'naïve' delimitation strategies under a range of dispersal scenarios and find it to be efficient and accurate, even with major data limitations (unknown time of invasion, unknown dispersal kernels, stochastic establishment dynamics and spatial heterogeneity), except at very low invasion densities. Early detection/rapid response initiatives are becoming firmly incorporated in integrated management strategies in many parts of the world, and further inputs along the lines of Leung *et al.* (2010) are urgently needed to guide these interventions.

THE BIOGEOGRAPHY OF CLIMATE CHANGE

Rapid climate change poses huge challenges for conservation managers. Despite an avalanche of studies in recent years aimed at predicting the response of species and ecosystems to predicted climate change, our knowledge of how important climate is in determining range limits (relative to many other factors) is inadequate for accurate modelling and forecasting (Whittaker *et al.*, 2005; Lozier *et al.*, 2009; Feeley & Silman, 2010). Thomas (2010) analysed the frequencies with which animal species have responded to climate change by shifting their range boundaries in the 'expected' direction (polewards). Results show that climate contributes to, but is not the sole determinant of, the locations of distribution boundaries for the majority of terrestrial species in continental regions. At the scale of landscapes, at which most practical control measures are implemented, the impacts of climate change, and biotic responses such as adaptation and migration, will be mediated by spatial heterogeneity in climate and climate change. Such complexity is generally ignored in modelling studies. Using surfaces of current climate and two scenarios of future climates, Ackerly *et al.* (2010) mapped disappearing, declining, expanding and novel climates, and the velocity and direction of climate change in California and Nevada. They also examined fine-scale spatial heterogeneity in protected areas of the San Francisco Bay Area in relation to reserve size, topographic complexity and distance from the ocean. Under the two climate change scenarios they considered, current climates across most of California and Nevada are predicted to shrink greatly in extent, and the climates of the highest peaks to disappear from the region. They predict that current temperature isoclines could move much faster in flatter regions than in mountainous areas because of the steep local topoclimatic gradients. In the San Francisco Bay Area, climate diversity within currently protected areas is predicted to increase with reserve size and proximity to the ocean. By 2100, of almost 500 protected areas (>100 ha), only eight of the largest are projected to experience temperatures within their currently observed range. Whilst great uncertainty must be attached to any such climate change models, these results are of heuristic value in suggesting that conservation strategies which prioritize the protection and connectivity of climatically heterogeneous landscapes and regions with declining climate extent should be supported.

TOWARDS ROBUST CONSERVATION BIOGEOGRAPHY – FRESHWATER FISHES EXAMINED

Every taxon and every region presents unique challenges to the conservation biogeographer. Freshwater systems are particularly complex environments and pose especially difficult problems for conservation planning. Olden *et al.* (2010) put forward 10 research challenges to advance our knowledge of the linkages between natural and human-induced environmental change and patterns of freshwater fish biogeography. Drawing on expertise from around the world, they propose a prospectus of key research questions addressing each challenge, including the need to test current and forge new theories in biogeography that can conserve information, advance a trait-based biogeography of freshwater fishes, quantify extinction risks and the geography of extinction debt for fishes, elucidate patterns and drivers of freshwater fish invasions and considerations relating to our ability to predict dynamics of freshwater ecosystems through enhanced understanding of the roles of multiple stressors.

CONSERVATION BIOGEOGRAPHY – THE ROAD AHEAD

While the general goal of conservation biogeography is to contribute to the scientific underpinnings of conservation decision-making, it is important to recognize that our science is produced within particular cultural contexts and that there will always be debate concerning which properties of nature we as a society wish to foster. For instance, we might wish to emphasize saving species from extinction as the prime goal, paying less attention to the assemblages and landscapes in which they occur. Or, we may wish to emphasize the importance of intact megafaunal assemblages, aesthetic and cultural significance of landscapes, ecosystem health, ecosystem services, or biotic integrity. Such differences in emphasis are linked to a similar diversity of social values motivating conservation action in many nations, especially at local scales, but also globally (Ladle & Whittaker, in press).

The decision to adopt a particular set of values is, traditionally, not within the bounds of science. However, in our view, biogeography is well poised to make a significant contribution in the coming years to the process of providing policy makers with alternative scenarios addressing differing end goals (cf. Williams & Araújo, 2002; Dimitrakopoulos *et al.*, 2004). To expand on this a little, any system of conservation prioritization, even if based on the application of numerical algorithms to comprehensive data sets, ultimately reflects value judgements as to what features are important and how to weigh them up (Knight & Cowling, 2007). Applying funding or protection to areas ranked highly by the chosen protocols may consequentially diminish opportunities for conservation elsewhere, perhaps including other areas of pressing conservation concern. On the scale of landscapes, regions and states, conservation biogeography is well placed to inform such choices. As the papers in this Special Issue illustrate, there are many exciting developments in play in the field, but also many complex and daunting challenges.

In their assessment of the field, Whittaker *et al.* (2005) highlighted four generic themes, which they felt required concerted attention: (i) scale dependency; (ii) inadequacies in taxonomic and distributional data; (iii) developing improved understanding of the effects of model structure and parameterization, through increased sensitivity analyses; and (iv) areas in which applied theory derived from biogeographical science required greater focused attention. Unsurprisingly, these areas remain pivotal to progress in our view. First, scale dependency is of central importance in assessing aspects of conservation biogeography as diverse as, for example, biodiversity pattern, the effects of anthropogenic influences generally, changes arising from the introduction of non-native species (e.g. Olden, 2006; Foxcroft *et al.*, 2009) and the criteria applied to assess the extinction risk assigned to plant or animal species (e.g. regarding the final topic, see: Abeli *et al.*, 2009; Martín, 2009). Second, as more and more genetic, taxonomic and distributional data are becoming available for analysis, we need to develop evermore sophisticated means of determining which components of diversity variation may be artefacts of collecting intensity or inadequacies of method, as opposed to 'real' pattern (see, e.g. Hopkins, 2007). Third, and intimately linked to our understanding of current distributions, we also need to deploy similar sensitivity analyses to a wide range of issues in modelling future processes and patterns of diversity change (e.g. Veloz, 2009; Willems & Hill, 2009; Feeley & Silman, 2010; Roura-Pascual *et al.*, 2010; Smolik *et al.*, 2010). Fourth, we highlight a continuing need for efforts to synthesize emerging findings within conservation biogeography and to update theory for the purpose of revising guidelines to practitioners. There is a tendency for many of us to seek to draw recommendations from particular case studies as we publish them, but as in many areas of human endeavour, a single case study may make for poor guidance, and hence the value of the sort of systematic reviews and syntheses presented by contributors to this Special Issue.

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